ANT DEFENCE OF COLONIES OF *APHIS FABAE* SCOPOLI (HEMIPTERA: APHIDIDAE), AGAINST PREDATION BY LADYBIRDS

CHRISTOPHER JIGGINS, MICHAEL MAJERUS* AND URSULA GOUGH

Department of Genetics, University of Cambridge, Downing Street, Cambridge CB2 3EH.

INTRODUCTION

The symbiosis of ants and honeydew-producing aphids is well studied (Way, 1963). Most myrmecophilous Homoptera show behavioural and structural modifications for life with ants. The ants eat honeydew, a waste product of the aphids. Honeydew is rich in carbohydrate and also contains free amino acids and amides (Ewart & Metcalf, 1956; Gray, 1952; Maltais & Auclair, 1952; Mittler, 1958), proteins (Maltais & Auclair, 1952), minerals and B-vitamins (Hagen, 1962). The ants may also obtain protein by preying on excess aphids in and around the colony (Nixon, 1951; Pontin, 1958). The assumed benefits to the aphids are primarily protection from natural enemies and improved hygiene through removal of honeydew and dead aphids. There is conflicting evidence concerning direct action by ants to defend aphids. El-Ziady & Kennedy (1956) showed that *Lasius niger* L. workers attacked and drove away larvae of *Adalia bipunctata* L., and adults of *A. bipunctata*, *Coccinella 7-punctata* L. and *Propylea 14-punctata* L. Banks (1962) observed that ants of this species remove coccinellid eggs from the vicinity of attended aphids. However, other workers have recorded that *L. niger* rarely interferes with adult coccinellids feeding on its attended aphids, Herzig (1938) and Wichmann (1955) both concluding that coccinellids preying on *L. niger*-tended aphid colonies are little affected by ants. A similar set of contradictory observations may be found in the literature on *Formica rufa* L. Wellenstein (1952) and Kloft (1953) report that only newly emerged or very old adult coccinellids were attacked, while Majerus (1989) reports adults of nine out of ten species of coccinellid, and larvae of two out of three species, were attacked and driven away by *F. rufa*. The one exception was that both larvae and adults of *Coccinella magnifica* Redtenbacher, a known myrmecophile (Donisthorpe, 1920, 1927, 1939), were ignored by the ants. Majerus (1989) suggests that this species uses pheromonal manipulation of the ants to allow it access to a large food source in the form of ant tended aphids.

Nixon (1951) concludes that any protection afforded aphids by their association with ants is only incidental, ants either accidentally disturbing some aphid predators or being naturally hostile to rapidly moving organisms including a number of aphid predators. More recently other authors (Way, 1963; Rotheray, 1989) have suggested that this is an over-simplification, and that the relationships between ants, aphids and aphid predators are more complicated and still little understood.

The aim of this project was to look at the behavioural interaction between ants and ladybirds.

METHODS

Fieldwork was carried out at Juniper Hall Field Studies Centre, Mickleham, Surrey, from 27 June to 3 July, 1991. A natural colony of *Aphis fabae* (black bean aphid)

*Addressee for correspondence.

on *Cirsium arvense* L. (creeping thistle) tended by *Myrmica ruginodis* Nylander was studied. There were approximately 40 ants on the aphid colony at any one time. A similar colony tended by *L. niger*—about six ants on the colony at any one time—was used for some preliminary tests and observations.

Ladybirds were collected from nettle beds in the vicinity of the Field Centre. They were kept in petri dishes for 1–2 days before the experiment. Ladybirds were starved prior to the experiment to ensure that they would be hungry and take an interest in the aphids. This standardized, at least to some extent, the nutritional status of the ladybirds.

A single ladybird was placed on the stem of the thistle 5 cm below the colony. Ladybirds are positively phototactic and negatively geotropic (Majerus & Kearns, 1989) so they tended to walk up the stem towards the colony. A variety of species of ladybird were used (see Table 1).

The results were recorded as a series of timed observations, noting, for example, each encounter between a ladybird and an ant, its position relative to the aphid colony, and the result of the encounter.

The experiment ended when the ladybird walked or flew off the plant, or went into a prolonged state of inactivity away from the colony. If it cleaned itself after an encounter with an ant, this was recorded. Sometimes the ladybird would start food-searching behaviour away from the colony without encountering an ant or aphid. This was recorded and the experiment ended by removing the ladybird. Another individual was then placed on the stem. Virtually all aphid colonies in the vicinity were tended by ants; however, one similar but untended aphid colony was found and this was used to carry out a small run of experiments as controls.

Table 1. Number of experiments with each species of coccinellid used. The finding of only one untended aphid colony meant that few control tests could be conducted.

		Experiments	Controls
Carnivorous species			
Adults			
Adalia bipunctata	(2-spot ladybird)	21	5
Coccinella 7-punctata	(7-spot ladybird)	13	4
Calvia 14-guttata	(cream-spot ladybird)	5	
Propylea 14-punctata	(14-spot ladybird)	5	
Myrrha 18-guttata	(18-spot ladybird)	3	
Anatis ocellata	(eyed ladybird)	1	
Exochomus 4-pustulatus	(pine ladybird)	2	
Myzia oblongoguttata	(striped ladybird)	2	
Non-carnivorous species			
Halyzia 16-guttata	(orange ladybird)	5	
Micraspis 16-punctata	(16-spot ladybird)	2	
Psyllobora 22-punctata	(22-spot ladybird)	8	
Larvae			
Adalia bipunctata	(2-spot ladybird)	5	
Coccinella 7-punctata	(7-spot ladybird)	4	
Anatis ocellata	(eyed ladybird)	3	

Two different aspects of the attack behaviour of the ants when they encountered a ladybird were recognized and recorded; (i) one or more ants managed to grab hold of the ladybird; and (ii) one or more ants squirted formic acid at the ladybird, recognizable when an ant curls its abdomen under its body towards the ladybird. This was often difficult to see and may not have been recorded in all cases. A variety of ladybird behaviours were recorded (see Table 3).

Each encounter, defined as contact between an ant and a ladybird which had not been in contact with any ants for the previous 10 seconds, was recorded. This was designed to eliminate cases when ants came in to help or to take over from others which had already attacked.

Each encounter was scored as either 'investigate' or 'escalate'. Investigate indicates that the ant touched the ladybird, generally with its antennae, but did not fight. Escalate indicates that the ant did attack. Attacks generally took the form of biting at the elytra or legs, squirting formic acid, or pushing to try to dislodge the ladybird. It should be noted that our analysis does not take into account the duration or ferocity of the attack—it only analyses the initial decision to attack.

Hypothetically, this decision will depend on the ants making some assessment of the threat to their food supply, in this case the colony of aphids, which in turn could depend on a variety of factors: how valuable the food source is, whether the food is scarce or abundant, how far the food source is from the ants' nest, and how close the predator is to the colony. To assess this final factor, encounters were divided into those before the ladybird reached the colony and those while the ladybird was actually on the colony.

Once a ladybird had been found on the colony the ants seemed to become more active and attack. To assess this the encounters between ants and ladybirds on the colony were split into those within the first 2 minutes after contact with the colony and those more than 2 minutes after initial contact. Two minutes were chosen arbitrarily.

As a large number of repeat experiments were conducted on the same colony there is a possibility that the ants' basic level of hostility changed during the day—this did not appear to be the case, but it is a possible criticism of the method used.

RESULTS

Summary of observations

A summary of the results of encounters between ants and ladybirds is given in Table 2. Typically, when introduced onto a stem, the ladybird ran up and reached the colony of aphids fairly quickly. In most cases the encounter with an ant occurred after the ladybird had reached the colony. The ant first palpated the ladybird with its antennae. In many cases the ants then escalated to attack behaviour. Other ants often joined in the attack, up to five being seen attacking at one time. Each ant only persisted with an attack for about 30–60 seconds, although continual recruitment of new ants meant that ladybirds were often under sustained attack for several minutes. In cases where an ant managed to secure a hold on the ladybird with its mandibles, usually on a leg, the ant's attack was often sustained for longer, in one case for 14 minutes.

It appeared that the elytra of adult ladybirds are defensively very effective against ants and, in our experiments, ants only gained an effective hold on six of the 67 ladybirds used.

In cases where an ant encountered a ladybird with an aphid in its mandibles, the ant tended to concentrate on retrieving the aphid rather than attacking the ladybird. This was despite that fact that the aphid was often already fatally injured.

Table 2. Details of ladybirds which successfully ate aphids. Results are only for carnivorous ladybird species.

(1) On the colony	two of 52 ladybirds (4%) ate an aphid from a colony tended by ants.
	five of nine ladybirds (56%) ate an aphid from the colony not tended by ants.
	five of 52 ladybirds got hold of an aphid but had it retrieved by the ants.
(2) Away from the colony	five of 52 ladybirds (10%) ate an aphid away from the colony.
	one of 52 ladybirds got hold of an aphid away from the colony but had it retrieved by ants.

(Aphids away from the main colony were either winged individuals walking on the leaves of the plant or sessile individuals feeding away from the colony).

Note: 26 ladybirds out of 52 reached the colony.

The results for the 'ladybird success rate' (see Table 2) show the enormously reduced success rate of ladybirds when the aphids had ants in attendance, compared with the control colony.

In order to determine the nature of the stimulus that induces ants to attack, a 'pseudo-ladybird' was made out of Blu-Tack and coloured red and black. This was stuck onto the thistle to see how the ants responded. It was totally ignored by the ants, even when an aphid was squashed in the process of putting it onto the plant. This suggests that it is either the movement of the ladybird or a chemical stimulus from the ladybird that provokes the attack and not just the presence of a foreign body on the aphid colony.

Table 3. Summary of results of experiment for all ladybird species, including non-carnivores, combined.

	Larvae	Adults	Control
Reaches aphid colony	5	31	6
Encountered ant(s)	8	44	—
Ant grabbed ladybird	2	6	—
Ant squirted acid	1	8	—
Ladybird dropped off	2	9	—
Ladybird clamped down	—	8	—
Ladybird returned to colony	—	5	—
Ladybird flew off	—	22	1
Ladybird stayed away	6	27	4
Ladybird ate an aphid on colony	0	2	5
Ladybird ate an aphid away from the colony	2	5	0
Total individuals used	12	67	9

The response of ladybirds to ant attacks varied between species. These differences are summarized later. In general ladybirds either clamped down as soon as attacked, presumably to prevent ants gaining an effective hold on them, or they moved away from the colony. In some cases the ladybirds only moved a short distance from the colony, returning to it once the ant attacks had subsided. In other cases, the ladybirds moved further from the colony and did not return.

After a sustained attack, and especially if squirted with formic acid, the ladybird often escaped up a leaf and clamped down for several minutes before starting to clean itself. This self-cleaning took several minutes on and off, the duration of cleaning being longer when they had been sprayed with formic acid.

One ladybird defence mechanism is 'reflex bleeding' (Majerus & Kearns, 1989). When attacked, a pungent yellow fluid is exuded from pores in the ladybird's legs, from where it runs along channels to the edge of the pronotum or elyta, where it forms small droplets. This defence was not used by the adult ladybirds against the ants in any of our experiments. On the other hand, the ladybird larvae did reflex bleed in response to sustained ant attacks. The reflex blood was secreted mainly from the 1st, 2nd, 8th and 9th abdominal segments, although other points of secretion were seen and it is possible that a secretion can be at any attack point on the abdomen, or at the base of the legs. It appeared to be used as a last-ditch defence against prolonged attacks. This may be because it reduced mobility as it tended to foul-up the larva's legs. Individual larvae only produced large amounts of fluid once, implying that the reservoir of fluid available at any time is limited. Indeed, it has recently been shown that adult *A. bipunctata* and *C. 7-punctata* only have a limited supply of reflex blood (de Jong et al., 1991; Holloway et al., 1991).

The failure of adults to reflex bleed in response to ant attacks probably indicates first, that reflex blood is a valuable resource which is costly to replenish, and secondly, that ants are not a serious threat to adult ladybirds, at most depriving them of a meal and costing them cleaning time. On the other hand, larvae, with their softer exoskeletons, are far more vulnerable to ant attacks, and are more likely to be killed (Majerus, 1989). Their use of reflex bleeding against ants is presumably a reflection of this greater vulnerability.

In terms of ladybird success, that is a ladybird actually managing to eat an aphid, a summary of the results is given in Table 2. For carnivorous ladybirds, the success rate on ant-tended aphid colonies was significantly lower than on the untended colony ($\chi^2_1 = 19.84$, $P < 0.001$ with Yates' correction). (This test uses totals released onto plants rather than just the number which reached the colony because it was noted that presence of ants on a plant could prevent the ladybird reaching the colony.) This result shows that ants do significantly reduce the effect of predation by ladybirds on aphid colonies. That five aphids were eaten by ladybirds on the plant supporting ant-tended colonies, but away from the main colony, suggests that first, it is ordinarily the main colony that the ants defend, and secondly, there is a considerable advantage to aphids in remaining within the main colony, in terms of reduced risk of predation.

The results of the ants' responses to ladybirds in terms of investigation and escalation are given in Table 4. The level of ant response before the ladybird reaches the colony can be used as a basic level of hostility before the ladybird has posed a direct threat to the aphid colony. Statistical comparisons of this base level with the level of response in the other classes show that the proportion of ants which escalate attacks is significantly increased while the ladybird is on the aphid colony ($\chi^2_1 = 13.18$, $P < 0.001$), and during the first 2 minutes after the ladybird has left the aphid colony ($\chi^2_1 = 7.29$, $P < 0.01$). However, there is no significant difference between the base

Table 4. Summary of the responses of ants on encountering ladybirds (carnivorous and non-carnivorous species combined).

Ant response	Before ladybird reaches colony	While ladybird is on colony	0–2 mins after ladybird has left colony	>2 mins after ladybird has left colony
Investigated, then escalated	11	33	18	15
Investigated only	18	8	6	15

level of response and the level more than 2 minutes after the ladybirds have left the colony ($\chi_1^2 = 0.87$, $P > 0.1$). Notably, there is also no significant difference between the level of ant response to ladybirds on the colony and in the first 2 minutes after the ladybirds have left the colony ($\chi_1^2 = 0.27$, $P > 0.1$). We conclude that there is a significant increase in ant hostility when the ladybird reaches the colony. This level of hostility begins to decrease some time after the ladybird leaves the colony and has effectively returned to the base level after about two minutes.

Species-specific notes

The above summary of results applies to most of the ladybird species used, but *A. bipunctata* and *C. 7-punctata* in particular. Although we did not do enough repeats to analyse the data statistically for differences between species, notes on the behavioural interactions of each species were made. Here follows a summary of these notes.

Propylea 14-punctata (14-spot ladybird)

On contact with ants, it employs a strange jolting action which appeared to be an attempt to shake ants from its back.

Myrrha 18-guttata L. (18-spot ladybird)

The ants seemed very aggresive towards this species and attacked continuously both before it reached the colony and afterwards on leaves at some distance from the colony. The ladybird continually ran away but the ants persisted in their attacks. It has been suggested that this species is a Scots pine specialist, breeding almost exlusively in the higher branches of mature trees (Majerus, 1988; Majerus & Kearns, 1989). It is feasible that by restricting reproductive activity, and in particular oviposition, to the tops of these tall trees, they avoid the extremely violent behaviour of the ants towards them. Why ants should react more aggressively to this species than others is not known.

Anatis ocellata L. (eyed ladybird)

When an ant managed to get hold of its leg the ladybird successfully dislodged the ant by kicking with its other legs. A larva of this species was the only ladybird which the ants successfully killed and carried off. Up to seven ants at a time carried the dead larva. The ants would lose interest for several minutes at a time and then start again, always moving the body down the plant.

Exochomus 4-pustulatus L. (pine ladybird)

This small ladybird has a rim around its elytra so that it fits very tightly against a flat substrate when clamped down. It is then almost impregnable. It clamped down very readily.

Myzia oblongoguttata L. (striped ladybird)

One of the two used successfully ate an aphid. Both stopped still when attacked and waited until the ants gave up rather than running away.

Non-carnivorous species

Halyzia 16-guttata L. (orange ladybird)

Very active and mobile. Made no attempt to clamp down when attacked, but ran away immediately and tried to fly. Although primarily a mildew feeder, the orange ladybird may eat small aphids when food is scarce (Majerus & Kearns, 1989). One of our specimens did grab hold of an aphid.

Micraspis 16-punctata L. (16-spot ladybird) and
Psyllobora 22-punctata L. (22-spot ladybird)

Neither of these species encountered aphids in the trials as they went straight up the nearest leaf each time, presumably as a result of different food searching behaviour associated with mildew feeding. Ants encountering these species treated them in the same way as carnivorous species.

Discussion

In our experiments, the ants are clearly vigorously defending the aphid colony. There is definitely more than just accidental disturbance of aphid predators. Nixon's (1951) conclusion of incidental protection of the aphids, is not borne out by our experiments.

Way (1963) summarized three reasons why ants may attack other insects: (1) if the ant is a predatory species which would be expected to attack most insects in their foraging territories; (2) if other insects are hostile to the ants themselves, and (3) if the other insect intrudes on the nest or on a food source which the ant is monopolizing.

The attacks in our experiments are clearly not a predatory effect as the ladybird is rarely physically injured, let alone killed. Also, if this were the case, one would expect an equal likelihood of attacks at any point on the plant. However, our ladybirds were often ignored when on leaves away from the colony, but attacked when near or on the aphid colony. The results for the ant response data also show this—the ants were far more likely to attack after the ladybird had reached the colony than before.

The ladybirds did not appear to be hostile to the defending ants, only to their attended Homoptera. We conclude that this is a case of ownership behaviour.

Variation in the assiduousness of the ants' tending of colonies may explain in part the ladybirds' strategy. There would at first appear to be little reason for the ladybird remaining on a plant after first encountering the ants. Their feeding success rate was minimal and they were liable to continual attacks from the ants. However, in view of the fact that the ladybirds are relatively immune to attack due to their protective elytra and that many tended colonies may not be so well defended, it may be worthwhile for the ladybird to stay and assess the situation and decide whether to remain still and hope to continue feeding or to flee. Wichmann (1955) suggested that Coccinellidae are adapted to attacking ant-tended colonies by keeping still when molested. It is also interesting to note that different species appear to be treated differently by the ants, some being attacked more violently than others. Our observations suggest a number of differences in the interactions between *M. ruginodis* and different ladybird species. These should be investigated further.

The ant response results show an increased level of ant hostility after the ladybird has been found on the colony and for about 2 minutes after it has left the colony. This result was suported by observational evidence; for example, on the colony tended by *L. niger*, after the ladybird had been found on the plant, the ants would sometimes all leave the colony to search for the ladybird, for several minutes. This was the only time we saw the colony untended during the day.

There could be a number of explanations for these observations; a pheromonal messenger, causing the increase in hostility, could be released either by the ants which encounter the ladybird or by the aphids themselves. This could either be released into the air, in which case it might take several minutes for levels to fall below a threshold value sufficient to stimulate the ants; or it could be released directly onto the ladybird, in which case the formic acid used by the ants is a possible candidate. The latter should seem less likely as the effect seems to be a more general increase in ant activity rather than a specific increase in hostility to the ladybird. This needs to be tested experimentally.

Acknowledgements

We are indebted to Mr John Bebbington, the Field Studies Council and the staff at Juniper Hall Field Studies Centre for their help and the use of their facilities. We also thank Maureen Blake and Joanne Griffiths for their typographical services.

References

Banks, C. J. 1962. Effects of the ant *Lasius niger* (L.) on insects preying on small populations of *Aphis fabae* (Scop.) on bean plants. *Ann. Appl. Biol.* **50**: 669–679.

de Jong, P. W., Holloway, G. J., Brakefield, P. M. & de Vos, H. 1991. Chemical defence in ladybird beetles (Coccinellidae). II. Amount of reflex fluid, the alkaloid adaline and individual variation in defence in 2-spot ladybirds (*Adalia bipunctata*). *Chemoecology* **2**: 15–19.

Donisthorpe, H. St J. K. 1920. The myrmecophilous ladybird *Coccinella distincta*, Fald., its life-history and association with ants. *Ent. Rec. J. Var.* **32**: 1–3.

Donisthorpe, H. St J. K. 1927. *The guests of British ants; their habits and life-histories*, London, Routledge.

Donisthorpe, H. St J. K. 1939. *A preliminary list of the Coleoptera of Windsor Forest*. London.

El-Ziady, S. & Kennedy, J. S. 1956. Beneficial effects of the common garden ant *Lasius niger* L., on the black bean aphid, *Aphis fabae* Scopoli. *Proc. Roy. Ent. Soc. Lond. (A)* **31**: 61–65.

Ewart, W. H. & Metcalf, R. L. 1956. Preliminary studies of sugars and amino-acids in the honeydews of five species of coccids feeding on citrus in California. *Ann. Entomol. Soc. Am.* **47**: 441–447.

Gray, R. A. 1952. Composition of honey-dew excreted by pineapple mealy bugs. *Science* **115**: 129–133.

Hagen, K. S. 1962. Biology and ecology of predaceous Coccinellidae. *Ann. Rev. Ent.* **7**: 289–326.

Herzig, J. 1938. Ameisen and Blattlause. *Z. Angew. Entomol.* **24**: 367–435.

Holloway, G. J., de Jong, P. W., Brakefield, P. M. & de Vos, H. 1991. Chemical defence in ladybird beetles (Coccinellidae). I. Distribution of coccinelline and individual variation in defence in 7-spot ladybirds (*Coccinella septempunctata*). *Chemoecology* **2**: 7–14.

Kloft, W. 1953. Waldameisen und Pflanzenläuse. *Allgem. Forstz.* **8**: 529.
Majerus, M. E. N. 1988. Some notes on the 18-spot ladybird (*Myrrha 18-guttata* L.) (Coleoptera: Coccinellidae). *Br. J. Ent. Nat. Hist.* **1**: 11–14.
Majerus, M. E. N. 1989. *Coccinella magnifica* (Redtenbacher): a myrmecophilous ladybird. *Br. J. Ent. Nat. Hist.* **2**: 97–106.
Majerus, M. E. N. & Kearns, P. W. E. 1989. *Ladybirds. Naturalists' Handbooks 10*, Slough, Richmond Publishing.
Maltais, J. B. & Auclair, J. L. 1952. Occurrence of amino-acids in the honey-dew of the crescent-marked lily aphid *Myzus circumflexus* (Buck.). *Can. J. Zool.* **30**: 191–193.
Mittler, T. E. 1958. Studies on the feeding and nutrition of *Tuberolachnus salignus* (Gmelin). II. The nitrogen and sugar composition of ingested phloem sap and excreted honeydew. *J. Exptl. Biol.* **35**: 626–638.
Nixon, G. E. J. 1951. *The association of ants with aphids and coccids*. London, Commonwealth Inst. Entomol.
Pontin, A. J. 1958. A preliminary note on the eating of aphids by ants of the genus *Lasius*. *Entomologist's Mon. Mag.* **94**: 9–11.
Rotheray, G. E. 1989. *Aphid predators. Naturalists' Handbooks 11*, Slough, Richmond Publishing.
Way, M. J. 1963. Mutualism between ants and honey-dew producing Homoptera. *Ann. Rev. Ent.* **8**: 307–344.
Wellenstein, G. 1952. Zur Ernährungsbiologie der Roten Waldameise (*Formica rufa* L.) *Z. Pflanzenkrankh. u. Pflanzenschutz* **59**: 430–451.
Wichmann, M. E. 1955. Das Schutzverhalten von insekten gegenüber Ameisen. *Z. Angew. Entomol.* **37**: 507–510.

BOOK REVIEW

The Lepidoptera by Malcolm J. Scoble. Natural History Museum Publications/ Oxford University Press, 1992, ISBN 0-19-854031-0, 404 pages (4 colour plates and 321 figures and black and white photographs) £45, hardback.—A glance around the "natural history" section of any book shop will reveal a wide range of books on bufferflies and moths. Most, if not all, will be identification guides, although a few will have some pages on other matters such as their ecology and structure. There has, until now, been a noticeable lack of any up to date book on the form, function and diversity of the Lepidoptera. This void has been filled with the publication of M. Scoble's *The Lepidoptera* (earlier volumes in the series have been published on the Hymenoptera and Hemiptera).

The book's text is divided into three sections. The first part deals with the form and function of the external lepidopteran morphology, i.e. the head, thorax and abdomen, followed by chapters, on the same subject matter, on the ova, larvae and pupae, with the concluding chapter on "hearing, sound and scent". The initial chapters describe the morphology of each body section and their associated structures, followed by a detailed description of the function of the structures. I would recommend that any reader with a passing interest in the Lepidoptera, reads Chapter 2, which deals with the insect's head and amongst other things, feeding mechanisms and habits. The reader's attention should focus on the feeding habits of the Noctuid genus *Calyptra*. This genus includes species which feed on fruit by piercing the skin and one species, *C. eustrigata*, which feeds on mammalian blood. A fascinating description is given of the piercing mechanism, which is apparently confined to the males.

The wings are given extensive treatment in Chapter 3 "The adult thorax", as is proper considering their importance. Their function is discussed in great detail. The